Growth pattern of the maxillary sinus in the Japanese macaque (Macaca fuscata) : reflections on the structural role of the paranasal sinuses

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Growth pattern of the maxillary sinus in the Japanese macaque (Macaca fuscata): reflections on the structural role of the paranasal sinuses

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ABSTRACT

To investigate the claim that the primate paranasal sinuses possess not a functional but a structural role associated with the skull architecture (Blaney, 1990), the relationship between the maxillary sinus and the skull architecture was studied ontogenetically in 30 skulls of male and female Japanese macaques (Macaca fuscata). Coronal CT scan series and computerised 3-dimensional images served to evaluate the maxillary sinus. The definitive hemispherical shape of the sinus was already achieved after the completion of the primary dentition. Sinus volume increased with a trend indicating positive allometry. When compared with an ontogenetic data set of orang-utan (Koppe et al. 1995), however, the growth rate of the maxillary sinus of M. fuscata was significantly less. The maxillary sinus both of male and female macaques enlarged according to a common growth pattern. However, no sexual dimorphism could be established for the maxillary sinus size. Although the volume of the right maxillary sinus was normally bigger than that of the left side, the results suggested that asymmetry in maxillary sinus volume is related neither to skull size nor sex. Whereas a correlation analysis showed close relationships between the maxillary sinus volume and external cranial dimensions, the partial correlation coefficients revealed that these relationships were highly influenced by skull size. Although it cannot be ruled out that the paranasal sinuses are to some extent linked to the skull architecture, this study does not support a solely structural role for these air cavities.

Key words: Craniofacial growth; sexual dimorphism; computed tomography.

INTRODUCTION

The actual function of the paranasal sinuses, as well as the factors involved in the pneumatisation of the facial skeleton, are still largely uncertain. Numerous authors have suggested that the development and growth of the air cavities are directly linked to both growth of the skull and dentition (e.g. Sperber, 1980; Wolf et al. 1993). Consequently, it is widely believed that the morphology of the paranasal sinuses in adults depends on the skull architecture and that the air cavities are designed to replace functionless bone between the bony pillars of the facial skeleton (Weidenreich, 1924; Lund, 1988).

The degree of pneumatisation, however, varies considerably among primate species. Furthermore, there is evidence that the difference in the maxillary sinus size between the Hominoidea and Old World monkeys cannot be explained only by a single factor such as body size (Koppe & Nagai, 1995). This also holds true for the morphology of the floor of the maxillary sinus. Although the relationships between the floor of the sinus and the posterior maxillary teeth tend to become closer in the large-sized hominoids (Ward & Pilbeam, 1983), root apices of the maxillary molars exposed into the sinus floor can also be found in relatively small-sized macaques such as M. mulatta (Koppe & Nagai, 1995).

While numerous authors have increased our understanding about the development, growth and variability of the human paranasal sinuses (e.g., Schaeffer, 1920; Leicher, 1928; Negus, 1958; Takahashi, 1983;...
Lang, 1989; Anon et al. 1996), the knowledge about the primate paranasal sinuses is still incomplete. Even though the morphology of the paranasal sinuses of the great apes and of certain Old and New World monkey species has been described in detail (Seydel, 1891; Paulli, 1900; Wegner, 1936; Cave & Haines, 1940; Cave, 1968, 1973), quantitative analyses of the primate paranasal sinuses are rare and mostly restricted to adult samples (Blaney, 1986; Lund, 1988; Koppe & Schumacher, 1992). As to our knowledge, except for a single report of the maxillary sinus in growing Bornean orang-utans (Koppe et al. 1995), there are no studies on the growth pattern of the air cavities in primates. This knowledge, however, is necessary to illuminate the role of the primate paranasal sinuses.

Thus the present study was performed to analyse the postnatal growth pattern of the maxillary sinus in a species of Old World monkey. The maxillary sinus is the only true air cavity of Old World monkeys (Koppe & Nagai, 1995). For this study, the Japanese macaque was chosen because the postnatal craniofacial growth as well as the dentition of this macaque is quite well known (Ikeda & Watanabe, 1966; Iwamoto et al. 1984, 1987; Mouri, 1994, 1995). Moreover, a preliminary study of adult Japanese macaques (Koppe et al. 1996a) revealed a relatively small degree of sexual dimorphism in the maxillary sinus size and suggested that both the size and shape of the maxillary sinus are less related to the external architecture of the skull than in hominoids. Therefore, this study may also verify whether the obvious differences in the morphology of the maxillary sinus between the Old World monkeys and Hominoidea are also reflected by differences in the postnatal growth pattern of this sinus.

Materials and Methods

Thirty skulls of the Japanese macaque (Macaca fuscata) of both sexes and of different ages were studied. The samples comprise skulls from both captive and wild animals. Because the age of death of none of these monkeys was known, their age was estimated from the tooth eruption sequence (Iwamoto et al. 1984, 1987; Mouri, 1994). The samples were divided into 4 age groups. Each age group was comprised of an equal number of male and female skulls: (1) deciduous dentition and fully erupted permanent 1st molar (6 animals); (2) fully erupted permanent incisors, as well as the permanent 2nd molar (6 animals); (3) fully erupted premolars (8 animals); and (4) complete secondary dentition (10 animals). According to Iwamoto et al. (1984, 1987) and Mouri (1994) these age groups range approximately as follows: (1) from birth to 2 y; (2) from 2 y to 4 y; (3) from 4 y to 4.5 y (female) and 4.75 y (male); (4) older than 4.5 and 4.75 y, respectively.

The skulls were scanned by CT in the coronal plane using a HiSpeed Advantage RP computed tomograph (General Electric Medical Systems, Milwaukee, USA). The slice thickness ranged from 0.5 to 1.0 mm, and the scanning parameters were 120 kV and 150 mA. The smaller slice thickness was applied to the skulls of the age group 1 in order to increase the accuracy of the following 3-dimensional (3D) reconstructions (Lofchy et al. 1994). In addition, a number of broken skulls of newborn and infant monkeys, showing the maxillary sinus, were examined visually.

The serial coronal CT images were analysed with the ALLEGRO software program (ISG Technologies, Toronto). The ALLEGRO workstation was used to reformat the original coronal CT images of the skull to view the air cavities also in the sagittal and horizontal planes. This procedure also permits evaluation of the maxillary sinus and its relationship to neighbouring structures from a different perspective without the need to rescan the skulls. Furthermore, the ALLEGRO workstation served to perform 3D image reconstructions of the maxillary sinus and corresponding bony structures as well as for calculation of the maxillary sinus volume (Koppe et al. 1996a).

In addition, to determine the relationship between the maxillary sinus and skull architecture, the following linear measurements of external cranial parameters were recorded with a sliding caliper (Mitutoyo, Tokyo): basicranial length (basion to nasion); facial length (basion to prosthion), palatal length (prosthion to staphyion), biorbital width (frontomalare temporoal to frontomalare temporale); and bimaxillary width (zygomaxillare to zygomaxillare) (Fig. 1).

Dean & Wood (1981) emphasised that cross-sectional data of any kind do not permit the demonstration of individual differences in the rate of growth or the timing of particular events within the growth period. Thus, because the exact ontogenetic ages of the samples were not known and in view of the small sample size, the relative growth of the maxillary sinus was described using the basicranial length as an independent variable. The basicranial length is considered to be a valuable measure of overall skull size (Leutenegger & Masterson, 1989). The relationship between the logarithmic transformed data was analysed using a simple regression analysis, and the difference in the slope of the regression lines between
Maxillary sinus growth

The least-squares regression model was also applied to describe the growth changes of the external measurements of the skull. The sexes were pooled for this analysis. Differences in the relative growth between the external measurements of the skull and the maxillary sinus size were detected by testing the differences in slope of the regression lines using the 2-tailed t test. To verify whether the relations between the maxillary sinus volume and the external measures of the skull were influenced by the skull size factor, in addition to Pearson’s correlation coefficients, the partial correlation coefficients were also calculated.

In order to demonstrate possible differences in the growth pattern of the air cavities between the Old World monkeys and Hominoidea, the relative growth of the maxillary sinus of the Japanese macaque was compared with that of the maxillary sinus of the orang-utan (Koppe et al. 1995). The basicranial length again served as an independent variable in both species and least-squares regression was applied to describe the relationship between the data sets.

There are numerous discussions regarding which regression model is appropriate to describe the relationship between 2 variables, especially for comparisons between species (Leutenegger & Larson, 1985; McKinney, 1988; Martin & Barbour, 1989; Martin, 1990). In this study the least-squares regression model was applied, because it regards X as an independent variable. The basicranial length was used as an independent variable mainly to describe the proportional enlargement of the maxillary sinus rather than to explain the sinus growth (e.g. Martin, 1990). On the other hand, however, there is also reason to treat the measure of body/skull size as an independent variable because body size itself is an important determinant of numerous physiological and ecological parameters (McKinney, 1988; Smith et al. 1995).

Regarding the interspecies comparison of maxillary sinus growth, it is noteworthy to draw attention to the fact that the relationship between the maxillary sinus...
volume and age in the orang-utan is most appropriately described by a nonlinear regression model (Koppe et al. 1995). The curvilinear pattern of the plotted data did not change significantly after the logarithmic transformation of the raw values. Thus the orang-utan’s data set was divided into 2 groups according to the growth pattern as described by Koppe et al. (1995): group 1, samples with age of less than 16 y; and group 2, samples older than 15 y of age. The differences in the slopes of the regression lines of the maxillary sinus of *M. fuscata* and the orang-utan were tested using the 2-tailed *t* test (*P* < 0.05).

The paranasal sinuses are subject of considerable variation in size and shape. Although prominent developmental anomalies of the maxillary sinus may occur either as hypoplasia or as aplasia (Bassiouny et al. 1982), asymmetry in the sinus usually arises as small random deviations from symmetry. This kind of asymmetry can be considered as so-called fluctuating asymmetry (Manning & Chamberlain, 1993). To reveal whether the observed asymmetry in maxillary sinus volume of *M. fuscata* is related to age or to sex, the absolute asymmetry was calculated as the difference in the volume of the left and right maxillary sinus (Manning & Chamberlain, 1993). Because there was a significant relationship between the absolute asymmetry and skull size of the males, the relative asymmetry between the right and the left maxillary volume was also calculated and expressed by an asymmetry index. As asymmetry index we adopted the size dimorphism index that was initially proposed by Lovich & Gibbons (1992) to express sexual size dimorphism. The asymmetry index (AI) used in this study is based on the size of the larger maxillary sinus (LMS) divided by the size of the smaller maxillary sinus (SMS). To exhibit directionality, the asymmetry index was calculated with the formula AI = [LMS/SMS] + 1 when the right maxillary sinus was larger or AI = [LMS/SMS] − 1 when the left maxillary sinus was larger. Arbitrarily the asymmetry index was defined as positive when the left maxillary sinus was larger and negative when the right maxillary sinus was larger.
RESULTS

The examination of a few isolated maxillary bones and broken skulls revealed that the maxillary sinus has already invaded the maxillary bone at the age of 3–5 mo. At this stage the maxillary sinus appeared as a bean-like cavity 5–7 mm in length, 3–4 mm in width and 3–4 mm in height. After completion of the primary dentition the paired maxillary sinuses emerged in the coronal CT scans as a nearly hemispherical cavity with the base towards the nasal cavity. At this stage the maxillary sinus was seen in the region of the 2nd maxillary deciduous molar and the tooth germ of the 1st maxillary molar. Only the latter, however, was in close relation to the maxillary sinus floor (Figs 2, 3).

As the permanent molars erupted the maxillary

Fig. 3. Three-dimensional images based on computerized reconstructions of coronal CT scans of Macaca fuscata in different age groups showing a part of the facial skeleton (grey) from the lateral aspect with the right maxillary sinus (red) and its relation to the developing permanent teeth viewed from laterally. The tooth roots of already erupted teeth are shown in red, whereas the tooth germs and the tooth roots of erupting permanent teeth are indicated in yellow. The 1st maxillary molar is always marked by an arrowhead. (a, b) Male macaques; (c, d), female macaques.
sinus gradually enlarged mainly in an anteroposterior direction. The growth laterally towards the zygomaticomaxillary suture was less pronounced. Thus in coronal CT scans the hemispherical form of the maxillary sinus, which was already evident with the completion of the primary dentition, did not change markedly. During the eruption of the secondary dentition the maxillary sinus came in contact with the crypts of the developing 2nd maxillary molar (Figs 2, 3). After the eruption of the permanent 2nd molar the maxillary sinus shared a wall with the crypt of the tooth germ of the 3rd maxillary molar (Fig. 3). Although the maxillary sinus was seen frequently in close proximity to the developing molars during the eruption of the secondary dentition, the tooth germs were not exposed as bulges into the sinus floor. After the completion of the secondary dentition, only the palatal root of the 1st maxillary molar occasionally reached the maxillary sinus floor (Fig. 3).

The maxillary sinus volume (pooled sexes) increased from 0.07 cm$^3$ in age group 1 to 0.88 cm$^3$ in age group 4 (adult) (Table 2). Although male monkeys tended to have a bigger sinus than female monkeys, there was no significant sexual dimorphism in sinus size. The plot of the log-transformed data against the basicranial length indicated that both male and female macaques follow the same growth pattern. Moreover the statistical analysis revealed no significant difference in the slope of the regression lines of male and female samples (Fig. 4).

Asymmetry between the right and left maxillary sinus volume also occurs in *M. fuscata*. Although

Table 1. Means and standard deviations of the maxillary sinus volume* of male and female Japanese macaques in different age groups

<table>
<thead>
<tr>
<th>Age group</th>
<th>Males</th>
<th></th>
<th></th>
<th>Females</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Right sinus</td>
<td>Left sinus</td>
<td></td>
<td>Right sinus</td>
<td>Left sinus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>Mean</td>
<td>s.d.</td>
<td>Mean</td>
<td>s.d.</td>
<td>AS</td>
</tr>
<tr>
<td>1</td>
<td>3</td>
<td>0.07</td>
<td>0.03</td>
<td>0.06</td>
<td>0.03</td>
<td>0.009</td>
</tr>
<tr>
<td>2</td>
<td>3</td>
<td>0.24</td>
<td>0.13</td>
<td>0.12</td>
<td>0.11</td>
<td>0.066</td>
</tr>
<tr>
<td>3</td>
<td>4</td>
<td>0.38</td>
<td>0.17</td>
<td>0.40</td>
<td>0.17</td>
<td>0.054</td>
</tr>
<tr>
<td>4</td>
<td>5</td>
<td>0.99</td>
<td>0.48</td>
<td>0.90</td>
<td>0.24</td>
<td>0.257</td>
</tr>
</tbody>
</table>

* In cm$^3$; n, sample size; the 2-tailed t test revealed no sex difference in maxillary sinus volume in any of these age groups; AS, absolute asymmetry, i.e. mean difference in the volume of the left and right maxillary sinuses.

Table 2. Means and standard deviations for right maxillary sinus volume* of *Macaca fuscata* and *Pongo satyrus borneensis* in different age groups, sexes are pooled. The relative increase of maxillary sinus volume is expressed as percentage from the age group 4 (adult)

<table>
<thead>
<tr>
<th>Age group</th>
<th>Macaca fuscata</th>
<th></th>
<th></th>
<th>Pongo satyrus borneensis</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Mean</td>
<td>s.d.</td>
<td>P</td>
<td>n</td>
</tr>
<tr>
<td>1</td>
<td>6</td>
<td>0.07</td>
<td>0.02</td>
<td>7.8</td>
<td>6</td>
</tr>
<tr>
<td>2</td>
<td>6</td>
<td>0.18</td>
<td>0.11</td>
<td>20.3</td>
<td>6</td>
</tr>
<tr>
<td>3</td>
<td>8</td>
<td>0.35</td>
<td>0.19</td>
<td>39.3</td>
<td>6</td>
</tr>
<tr>
<td>4</td>
<td>10</td>
<td>0.88</td>
<td>0.46</td>
<td>100.0</td>
<td>22</td>
</tr>
</tbody>
</table>

* In cm$^3$; * taken from Koppe et al. (1995); n, sample size; P, percentage.

Fig. 4. Bivariate logarithmic plot of the maxillary sinus volume against the basicranial length in male and female *Macaca fuscata*. Note that the values of both male and female monkeys form a common cluster.
Table 3. Regression coefficients for log-transformed right maxillary sinus volume and external cranial dimensions against basicranial length in Macaca fuscata; sexes are pooled. Asterisks mark slopes, significantly different from the slope of maxillary sinus volume

<table>
<thead>
<tr>
<th>Dimensions (n)</th>
<th>Intercept</th>
<th>Slope</th>
<th>95% CI</th>
<th>r</th>
<th>t value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maxillary sinus volume* (30)</td>
<td>−2.158</td>
<td>2.449</td>
<td>(1.806, 3.092)</td>
<td>0.828</td>
<td>—</td>
</tr>
<tr>
<td>Facial length (30)</td>
<td>−0.459</td>
<td>1.662</td>
<td>(1.566, 1.759)</td>
<td>0.989</td>
<td>2.483*</td>
</tr>
<tr>
<td>Palatal length (30)</td>
<td>−0.906</td>
<td>1.852</td>
<td>(1.510, 2.193)</td>
<td>0.903</td>
<td>1.677ns</td>
</tr>
<tr>
<td>Bimaxillary width (30)</td>
<td>−0.109</td>
<td>1.059</td>
<td>(0.917, 1.200)</td>
<td>0.945</td>
<td>4.330**</td>
</tr>
<tr>
<td>Biorbital width (30)</td>
<td>0.119</td>
<td>0.725</td>
<td>(0.574, 0.876)</td>
<td>0.882</td>
<td>5.345**</td>
</tr>
</tbody>
</table>

n, Sample size; *cube root value; 95% CI, 95% confidence interval for slope estimate; * P < 0.05; ** P < 0.01; "" not significant.

Table 4. Correlation matrix among the measurement items of the right maxillary sinus and external cranial measurement in growing Japanese macaques; sexes are pooled (n = 30)

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Maxillary sinus volume</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>2 Basicranial length</td>
<td>0.696</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>3 Facial length</td>
<td>0.736</td>
<td>0.987</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>4 Palatal length</td>
<td>0.701</td>
<td>0.906</td>
<td>0.926</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>5 Bimaxillary width</td>
<td>0.737</td>
<td>0.940</td>
<td>0.944</td>
<td>0.894</td>
<td>—</td>
</tr>
<tr>
<td>6 Biorbital width</td>
<td>0.677</td>
<td>0.870</td>
<td>0.874</td>
<td>0.770</td>
<td>0.885</td>
</tr>
</tbody>
</table>

For all results P < 0.01; n, sample size.

Table 5. Pearson’s correlation coefficients (r) and partial correlation coefficients (r’) among the maxillary sinus volume and external cranial dimensions. (Sexes are pooled, n = 30)*

<table>
<thead>
<tr>
<th>Dimensions</th>
<th>r</th>
<th>r’</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maxillary sinus volume (right)</td>
<td>0.954**</td>
<td>0.908**</td>
</tr>
<tr>
<td>Facial length</td>
<td>0.736**</td>
<td>0.423*</td>
</tr>
<tr>
<td>Palatal length</td>
<td>0.701**</td>
<td>0.046ns</td>
</tr>
<tr>
<td>Bimaxillary width</td>
<td>0.737**</td>
<td>0.335**</td>
</tr>
<tr>
<td>Biorbital width</td>
<td>0.677**</td>
<td>0.201**</td>
</tr>
</tbody>
</table>

* Basicranial length = constant; * P < 0.05, ** P < 0.01; "" not significant; n, sample size.

Fig. 5. The relationship between log basicranial length and asymmetry index in male and female Japanese macaques. Although the right maxillary sinus of both male and female animals tended to be larger than the left maxillary sinus, correlation analysis revealed that the degree of asymmetry was not associated with basicranial length, either in males or females.

there was no clear consistency with regard to the direction of asymmetry, in both male and female monkeys the larger maxillary sinus volume was generally observed on the right side. The absolute asymmetry, however, was more pronounced in male monkeys and tended to increase from age group 1 to age group 4 (Table 1). We found for males that the absolute asymmetry was significantly correlated with

the basicranial length (r = 0.652; P < 0.01). There was no significant correlation between the absolute asymmetry and basicranial length in female monkeys. To obtain an asymmetry pattern that is independent from the skull size factor, the relative asymmetry was calculated and expressed by the asymmetry index (Fig. 5). A correlation analysis revealed no significant association between the basicranial length and the asymmetry index either for males (r = 0.335) or females (r = 0.214), suggesting that asymmetry in maxillary sinus volume is related neither to sex nor age.

Comparing the relative growth of the maxillary sinus with the growth of different external measurements of the skull, it became evident that maxillary sinus volume increased with a steeper slope than most
of the cranial measurements. However, there was no significant difference in the slopes of the regression lines between maxillary sinus volume and palatal length (Table 3). While the Pearson’s correlation coefficients indicated significant associations between maxillary sinus volume and the external measures of the skull, the calculation of the partial correlation coefficients proved that most of the correlations were influenced by the bascranial length (Tables 4, 5).

Regarding the interspecies comparison of the relative growth pattern of the maxillary sinus, this study showed different results depending on the treatment of the raw data for the orang-utan. In the case when the orang-utan data set was treated as a single group, regardless of the curvilinear plot of the log-transformed values, no differences in the slopes of the regression lines between *Macaca* fuscata and the orang-utan could be found. However, the division of the orang-utan’s values into 2 groups as indicated above revealed obvious differences in the growth patterns between these species. Although the relative growth of maxillary sinus volume of both the Japanese macaque and orang-utan (group 1) showed positive allometry, maxillary sinus volume of the orang-utan increased within the 1st group with a significantly steeper slope. Because group 2 comprises mainly adult and mature samples of orang-utan, the increase of the maxillary sinus volume within group 2 was significant smaller when compared with the growth series of the Japanese macaque, and the slope of the regression line indicated isometry, i.e. the increase of maxillary sinus volume proportionally to bascranial length (Tables 2, 6).

**Discussion**

**Maxillary sinus growth**

Regarding the known variation in size and shape of the paranasal sinuses it is interesting to note that the definitive shape of the maxillary sinus is achieved in the Japanese macaque relatively early in postnatal development with the completion of the primary dentition. The finding that the characteristic pyramidal shape of the human maxillary sinus does not emerge before the eruption of the 2nd molar (Schaeffer, 1910) may point to species differences in the relationship of the maxillary sinus to the developing teeth. Indeed, Ward & Brown (1986) held that in cercopithecoids the development of the maxillary sinus is not closely synchronised with dental maturation as in man. The present study seems to support this claim.

Although the maxillary sinus floor of the Japanese macaque was always in close proximity to the tooth germs of the maxillary molars during postnatal growth, contrary to the condition found in the hominoids (Underwood, 1910; Schaeffer, 1920; Runge, 1928; Koppe et al. 1995), the crypts of the developing tooth germs of *M. fuscata* were not exposed as bulges in the walls of the maxillary sinus. When the eruption of the permanent teeth is completed, the differences between *M. fuscata* and the hominoids regarding the relationship of the maxillary sinus floor to the tooth roots are much clearer. Whereas in the hominoids the tooth roots of the maxillary posterior teeth are in close proximity to the floor of the maxillary sinus also after completion of the primary dentition, the sinus floor in adult Japanese macaques is usually seen quite far from the root apices of the molars (Koppe & Nagai, 1995). Numerous studies have highlighted the fact that the enlargement of the human maxillary sinus into the maxilla is restrained by the developing teeth (e.g. Anon et al. 1996). However, it is important to recall that also in man the influence of the primary dentition on the growth of the maxillary sinus is not conspicuous (Schaeffer, 1920; Runge, 1928).

At first glance the results of the morphological analysis seem to support the view of the maxillary sinus of Old World monkeys as a structure which, if present at all, expands very slowly and not to any great extent (Ward & Brown, 1986; Benefit & McCrossin, 1993). The results of this study showed, however, that the maxillary sinus volume increased with a trend indicating positive allometry, i.e. the

## Table 6. Comparison of the regression coefficients for log-transformed right maxillary sinus volume against bascranial length between *Macaca fuscata* and *Pongo satyrus borneensis*; sexes are pooled. Asterisks mark slopes of *Pongo satyrus borneensis* significantly different from *Macaca fuscata*.

<table>
<thead>
<tr>
<th>Species (n)</th>
<th>Intercept</th>
<th>Slope</th>
<th>95% CI</th>
<th>r</th>
<th>t value</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Macaca fuscata</em></td>
<td>−6.427</td>
<td>7.284</td>
<td>(5.344, 9.225)</td>
<td>0.824</td>
<td>—</td>
</tr>
<tr>
<td><em>Pongo satyrus</em>—G1 (24)</td>
<td>−8.132</td>
<td>9.889</td>
<td>(8.232, 11.546)</td>
<td>0.938</td>
<td>2.081*</td>
</tr>
<tr>
<td><em>Pongo satyrus</em>—G2 (16)</td>
<td>−2.567</td>
<td>1.852</td>
<td>(0.956, 4.177)</td>
<td>0.675</td>
<td>2.246ns</td>
</tr>
</tbody>
</table>

*Data from Koppe et al. (1995); n, sample size; Group 1, age 0–15 y, Group 2 age > 15 y; 95% CI, 95% confidence interval for slope estimate; * P < 0.05; ns not significant.
Sinus grew faster postnatally than did basicranial length. Although comparable data are rare, this growth pattern is similar to that of the maxillary sinus of man and the orang-utan (Libersa et al. 1981; Koppe et al. 1995). Moreover, the fact that frontal sinus volume in the African great apes also shows positive allometry when scaled relative to skull length (Blaney, 1986), suggests that this trend is a common pattern within higher primates. However, although the maxillary sinus both of the Japanese macaque and the orang-utan tended to increase with increasing skull size, this present study confirms an earlier report (Koppe & Nagai, 1995) which showed evidence that this relationship may differ in the hominoids and Old World monkeys.

Variation in size and shape of the paranasal sinuses is a common finding. In humans the maxillary sinuses are subject to fewer variations than the other paranasal sinuses (Dodd & Jing, 1977). The present study showed a significant correlation between the absolute asymmetry in maxillary sinus volume and skull size, but only for males. At first glance results seem to support the view (Manning & Chamberlain, 1983) that structures under stronger sexual selection tend to show a higher level of asymmetry. However, the asymmetry index (Fig. 5) revealed that neither skull size nor sex is correlated with asymmetry. Despite numerous studies concerning asymmetry in the size of the human maxillary sinus which differ mainly in whether the left (Anagnostopoulou et al. 1991; Nowak & Mehlis, 1975) or right maxillary sinus (Schürch, 1906; Schumacher et al. 1972) is larger, it has been suggested that asymmetry in the human maxillary sinus is usually very small (Ariji et al. 1994). Moreover Ariji et al. demonstrated that missing teeth did not affect the differences between the volume of the right and left maxillary sinuses. Although more studies are necessary to explore the influence both of environmental and genomic stress on the asymmetry in maxillary sinus size, the present study supports the assumption (Livshits & Smouse, 1993) that fluctuating asymmetry such as in maxillary sinus size might be considered merely as a ‘measure of noise’ in development.

Sexual dimorphism in maxillary size is well documented for both man and the great apes (Schaeffer, 1920; Nowak & Mehlis, 1975; Koppe et al. 1995). Recently Koppe et al. (1995) have suggested that sexual dimorphism in the maxillary sinus volume of the orang-utan results from prolonged growth in males. This pattern is the ontogenetic basis of sexual dimorphism of most external cranial traits of the Old World monkeys (Shea, 1986; Ravosa, 1991), including M. fuscata (Mouri, 1994). In the latter, sexual dimorphism of numerous cranial dimensions occurs in early stages of postnatal development (Mouri, 1994). The present study, however revealed a lack of sexual dimorphism in the maxillary sinus size. If both male and female Japanese macaques exhibit a common growth pattern in most of the external cranial dimensions as well as in the maxillary sinus, the question arises why does the growth of the maxillary sinus stop so early in males?

Blaney (1986), studying the sexual dimorphism of frontal sinus volume in African great apes, held that the external cranial morphology also has a considerable influence on the degree of sexual dimorphism in sinus size, i.e. the smaller the degree of sexual dimorphism in external cranial dimensions the smaller the dimorphism in sinus size. Although further studies on related species such as M. mulatta and M. fascicularis, which exhibit a stronger sexual dimorphism in most cranial dimensions than M. fuscata (Mouri, 1995), are necessary to evaluate the validity of Blaney’s (1986) approach for M. fuscata, the results of the present study suggest that the relationship between the morphology of the maxillary sinus of M. fuscata and the external cranial architecture is obviously weak. All calculated partial correlation coefficients between maxillary sinus volume and different measures of the skull were clearly below the Pearson’s correlation coefficients (Table 5). The lack of sexual dimorphism in the maxillary sinus size of M. fuscata as well as the weak relationship between the sinus and the external dimensions of the skull strengthen the assumption that the influence of facial growth on the development of the maxillary sinus is smaller than had been previously suggested (e.g. McGowan et al. 1993). These findings support earlier studies in man suggesting that the maxillary sinus possesses a developmental potential of its own (Schaeffer, 1920; Libersa et al. 1981).

The ‘structural’ role of the paranasal sinuses

Among primates, the maxillary sinus tends to enlarge with increasing skull/body size (Ward et al. 1982; Lund, 1988). Furthermore, in addition to a maxillary sinus that pneumatises virtually the whole maxillary bone, the African apes and man have the ethmoidal, frontal and sphenoidal sinuses. This high degree of skull pneumatisation seems to support Blaney’s (1986) claim that the paranasal sinuses do not have a functional but only a structural role, i.e. to eliminate unnecessary bone between the pillars of the facial skeleton. The lack of sexual dimorphism in sinus size
as well as the weak relationship between the external cranial architecture and the maxillary sinus in *M. fuscata* suggests, however, that a solely structural role of the maxillary sinus is questionable at least for this species. On the other hand, recent clinical studies indicate that the influence of external cranial morphology on pneumatisation in man is also obviously smaller than is usually indicated in common textbooks on human anatomy. Robinson et al. (1982) and Francis et al. (1990) have demonstrated that in patients with cleft palate neither size and shape nor the growth rate of the air cavities differed significantly from a normal population. Furthermore, recent investigations on Bornean orang-utans (Koppe et al. 1996b) strengthen the assumption that the influence of palatal form on the maxillary sinus is not conspicuous.

The numerous theories about the significance of the paranasal sinuses explain the air cavities either on a structural or a functional basis (for review see, Blanton & Biggs, 1969; Takahashi, 1983; Blaney, 1990). Although none of these theories have been convincingly proved, arguments supporting a structural role for the paranasal sinuses dominate the literature. With regard to biomechanical analysis of the skull morphology of different mammalian species (Demes et al. 1986; Preuschoft et al. 1986), Preuschoft (1989) claimed that the changes of skull shape during human evolution can be explained as an adaptation to the mechanical necessities caused by alterations of bite force. Moreover, he held that the widening of the maxillary sinus in hominoids can be understood as a possibly effective way to increase bending strength. Recent studies of in vivo bone strains in cercopithecoids (Hylander et al. 1991; Hylander & Johnson, 1992) have demonstrated, however, that not all bony structures of the face are designed to optimize strength according to the masticatory loads.

It is important to recall that the morphology of the skull as seen in adults is the result of complex interactions between its numerous skeletal subunits in the course of ontogenesis (Moss & Greenberg, 1967; McAlarney et al. 1992; Zelditch et al. 1992; Emerson & Bramble, 1993). Most of the growth-related allometric changes in size and shape of these subunits have functional consequences, which are also important in terms of phylogenesis (Dean & Wood, 1984; Emerson & Bramble, 1993). Thus with regard to the fact that the maxillary sinus is probably a primitive eutherian feature (Moore, 1981), it is unlikely that the primate air cavities have developed only because of alterations in skull morphology. Conversely, we hypothesise that the already present paranasal sinuses served during the evolution of hominoids as structures to optimise the skull architecture (e.g. Preuschoft, 1986).

Regarding the function of the paranasal sinuses, it should be stressed here that the sinus spaces have to be considered as part of the upper respiratory tract. Although there is considerable scepticism regarding a significant contribution of the paranasal sinuses, e.g. for air conditioning, it is interesting to note that the sinus mucosa shows a number of peculiarities such as a high regenerative capacity (McGowan et al. 1993) and a relatively high venous blood flow (Drettner & Aust, 1974). This blood flow is similar to that of the nasal mucous membrane and greater than in muscles, brain and liver (Drettner & Aust, 1974). It has been suggested that cooling of the nasal mucous membrane through ventilation may be important for the regulation of brain temperature (e.g. Baker & Chapman, 1977; Dean, 1988; Zenker & Kubik, 1996). In a recent paper, Zenker & Kubik (1996) claimed that among others the veins of the paranasal sinuses are involved in this process. Thus although it cannot be ruled out that the paranasal sinuses are in some way linked to skull architecture, we suppose that the paranasal sinuses are functional. These functions, however, may differ between different orders of mammals (Moore, 1981) and also among different taxonomic groups of primates.

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